EQUISETALES

Sporophytes with root, stem and leaves. Stems are jointed with whorls of leaves and branches at the nodes. The plant has unique stelar organization. Cones comprise peltate sporangiophores in whorls, bearing reflexed sporangia. The spores are homosporous and antherozoids are multiflagellate.

EQUISETUM

Equisetum, with some fifteen or more species, is distributed all over the world except Australia and New Zealand. It is commonly known as 'horse-tail' or 'scouring rushes'. The most conspicuous features of plant are jointed nature of stems (Fig. 4.1 A), intercalary growth, whorls of branches, small leaves around nodes, and sand papery texture. Due to sand papery texture *Equisetum* has been nicknamed as 'scouring rushes' and its whorls of branches make it look like the tail of a horse. The rough texture of plant is due to deposition of silica in cells on outer surface. Silica helps to protect the plant against predators and pathogens and prevents excessive water loss.

The plant with an interesting range of growth habits grows in a variety of habitats, ranging from wet places (ponds and marshes) to damp shaded places, along river banks, to exposed xeric conditions. *E. arvense* is the most common species. In some tropical localities, *Equisetum* is a weed and because of its poisonous contents is of concern to livestock owners. Horses are especially susceptible to its toxins. Some species accumulate minerals including gold (up to four and half ounce per ton). This feature of the plant is valuable in prospecting for new ore deposits.

All species have a perennial, subterranean, much branched, rhizome (Fig. 4.1 A) that helps the plant to spread prolifically. From the rhizome arise aerial axes, which are sparsely to highly branched. The aerial axes in *E. hyemale* are sparsely branched and develop dwarf branches in second or third year whereas they are highly branched in *E. sylvaticum* and *E. arvense*, showing branching of third or fourth order in the same year. In most species the aerial axes are of limited size (10-60 cm tall) but exceptionally *E. giganteum*, as the name suggests, may attain a height of 10-13 metres.

Some forms are evergreen, in others the aerial portions die back every year. Aerial stems in most species (Fig. 4.1A, B) are of two types, fertile and sterile. The former are colourless and unbranched with a strobilus at the apex. These appear before the sterile vegetative green axes with whorls of lateral branches. Exceptionally, in some species the fertile branches are green and may be branched or unbranched. In *E. pratense* the fertile shoot is green and after dispersal of spores gives rise to vegetative branches lower down. Also in *E. palustre* the fertile shoot is green and branched and every lateral branch ends in a cone. In species lacking heteromorphic branches i.e. *E. myriochaetum* and *E. debile* the cones are borne on normal green aerial branches.

The stems (rhizome and aerial axes) are ridged and differentiated into nodes and internodes. Around each node are small scale leaves (Fig. 4.1 A, B). The leaves are joined at their bases, forming a sheath around the node, and their free distal ends give the appearance of a frill. The leaves are normally of the same number as the ridges on stem. Each ridge corresponds to a leaf in the node above. Ridges in successive internodes alternate with one another and so also the leaves in successive leaf sheaths. As a departure from this regularity, the number of leaves diminishes in successive sheaths in the distal region of stem. It can be seen in a bud (Fig. 4.1 C, D). In Figure 4.1 C an outline diagram of cross section of bud are seen two whorls; the outer whorl has seven leaves and inner one has five. Two leaves which are nonalternating are massive, each with double leaf traces. Similarly, in Fig. 4.1 D, there are three whorls of eight, seven and five leaves, and nonalternating leaves are anomalous in size within their whorls. On this basis, an interesting generalization has been derived (Bierhorst, 1959). The nonalternating leaves, which are anomalous in size, frequently have double leaf traces

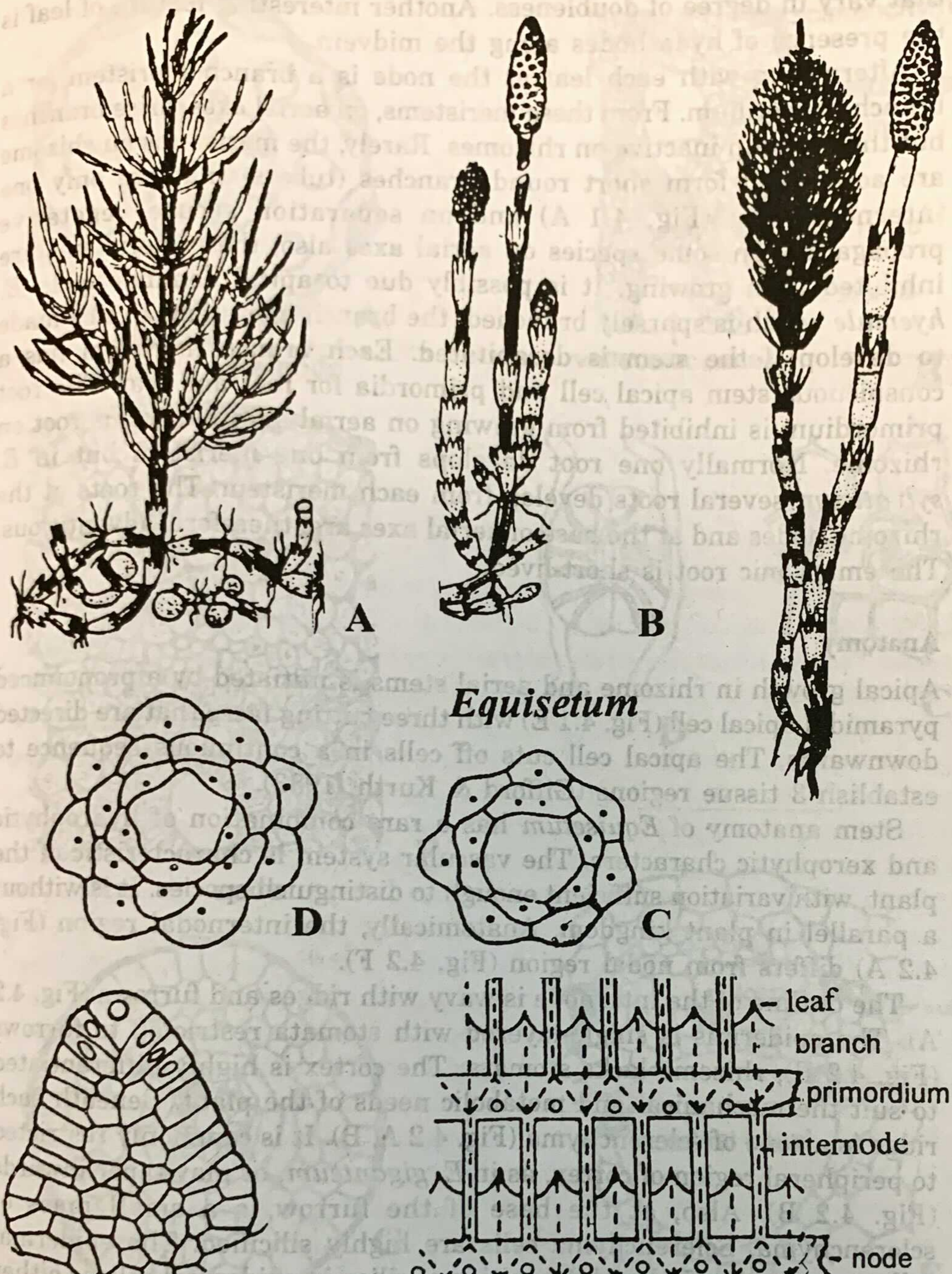

Fig. 4.1 *Equisetum*, morphology of sporophyte.

A, *E. arvense*, rhizome and aerial axes. B, *E. telmateia*, cone-bearing and vegetative axes. C,D, *E. palustre*, cross sections (diagrammatic) of bud showing concentric leaf whorls, around stem apex. E, shoot apex showing conspicuous apical cell and its derivatives. F, *E. arvense*, diagrammatic representation of node and internode.

that vary in degree of doubleness. Another interesting feature of leaf is the presence of hydathodes along the midvein.

Alternating with each leaf at the node is a branch meristem, or a branch primordium. From these meristems, on aerial axes, arise branches but they remain inactive on rhizomes. Rarely, the meristems on rhizome are active and form short round branches (tubers) that are only one internode long (Fig. 4.1 A) and on separation secure vegetative propagation. In some species on aerial axes also, these meristems are inhibited from growing. It is possibly due to apical dominance. In *E. hyemale* which is sparsely branched, the branch meristems can be made to develop if the stem is decapitated. Each branch meristem has a conspicuous stem apical cell and primordia for root and leaf. The root primordium is inhibited from growing on aerial axes but forms root on rhizome. Normally one root develops from one meristem but in *E. sylvaticum* several roots develop from each meristem. The roots at the rhizome nodes and at the base of aerial axes are, therefore, adventitious. The embryonic root is short-lived.

Anatomy

Apical growth in rhizome and aerial stems is initiated by a pronounced pyramidal apical cell (Fig. 4.1 E) with three cutting faces that are directed downwards. The apical cell cuts off cells in a continuous sequence to establish 3 tissue regions (Gifford & Kurth, 1983).

Stem anatomy of *Equisetum* has a rare combination of hydrophytic and xerophytic characters. The vascular system is characteristic of the plant, with variation sufficient enough to distinguish species. It is without a parallel in plant kingdom. Anatomically, the internodal region (Fig. 4.2 A) differs from nodal region (Fig. 4.2 F).

The outline of the internode is wavy with ridges and furrows (Fig. 4.2 A). The epidermis is single-layered with stomata restricted to furrows (Fig. 4.2 B), rhizome lacks stomata. The cortex is highly differentiated to suit the mechanical and metabolic needs of the plant. Beneath each ridge is a zone of sclerenchyma (Fig. 4.2 A, B). It is commonly restricted to peripheral region of cortex, as in *E. giganteum*, or may taper inwards (Fig. 4.2 B). Also, at the base of the furrow is a small mass of sclerenchyma. Sclerenchyma cells are highly silicified. The epidermal cells are also silicified and deposition of silica in epidermal cells is either in the form of discrete knobs or it covers the entire outer wall, giving the stem extremely rough texture. Silica substitutes for low lignin content of plant and is significant for erect texture. Silica is so essential for this plant that sporophytes developed in vitro from gametophytes formed viable spores only when the culture medium had at least 20 mg/L of silicon (Hoffman & Hillson, 1979).

Adjacent to the ridges and below the furrows are areas of cortical chlorenchyma (Fig. 4.2 B) with intercellular spaces, near the stomata. Since the leaves are small with few chloroplasts, cortical chlorenchyma

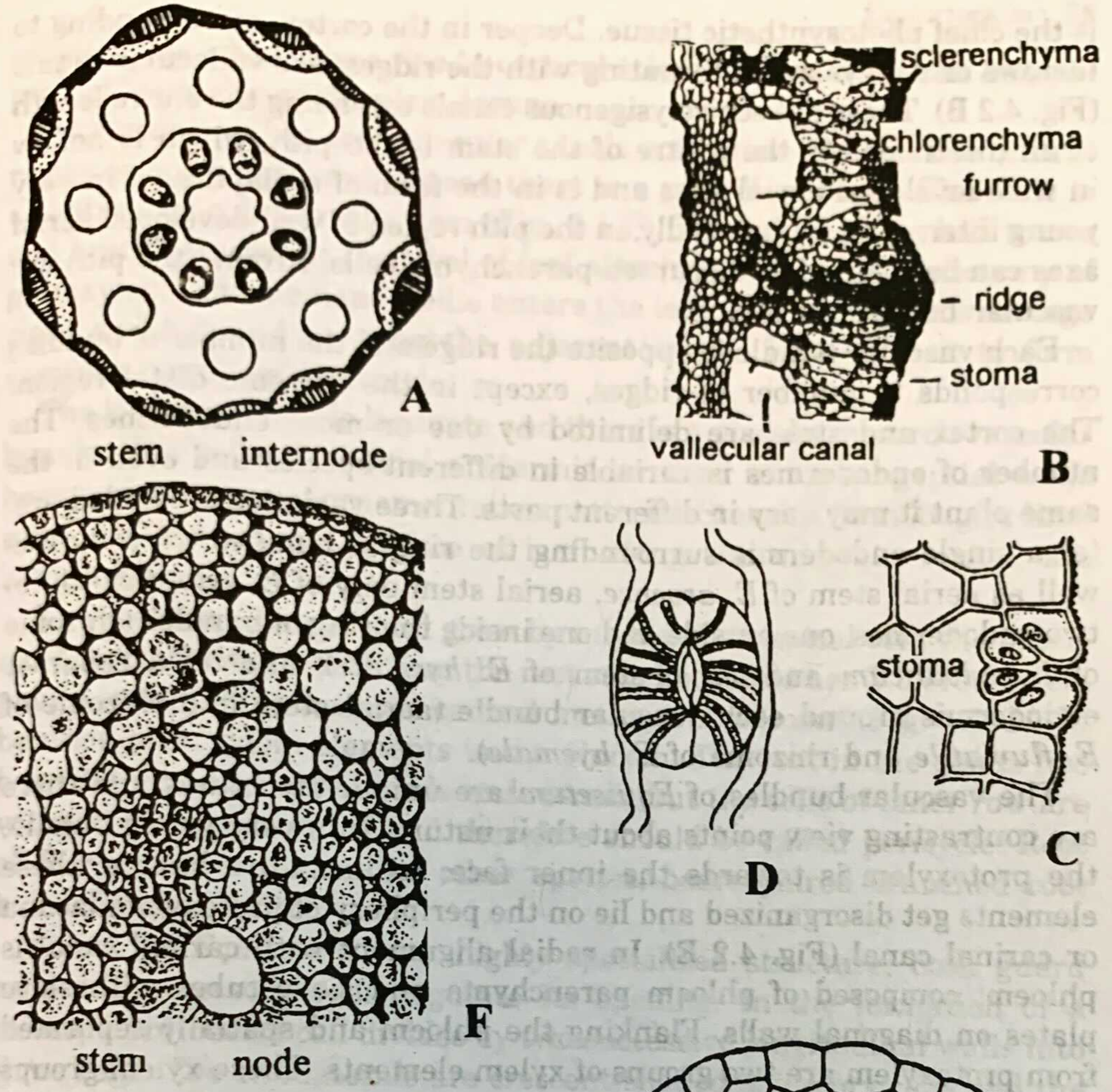

Fig. 4.2 *Equisetum*, anatomy of sporophyte.

A, *E. arvense*, transection (diagrammatic) of internode. B, *E. hyemale*, a portion of internode. C, *E. limosum*, vs of stoma. D, *E. telmateia*, inner face of stoma. E. *E. arvense*, a vascular bundle enlarged. F, *E. kansanum* ts of stem passing through intercalary meristem. G, *E. telmateia*, transection of root.

is the chief photosynthetic tissue. Deeper in the cortex, corresponding to furrows or valleys and alternating with the ridges, are vallecular canals (Fig. 4.2 B). These are schizolysigenous canals extending the entire length of an internode. At the centre of the stem is the pith, which is hollow in well-developed aerial axes and is in the form of a diaphragm in very young internodes. Occasionally, in the pith region of well-developed aerial axes can be seen a few disrupted parenchyma cells. Around the pith are vascular bundles in a ring.

Each vascular bundle is opposite the ridge and the number of bundles corresponds to number of ridges, except in the extreme distal region. The cortex and stele are delimited by one or more endodermes. The number of endodermes is variable in different species and even in the same plant it may vary in different parts. Three variations recorded are: (a) a single endodermis surrounding the ring of bundles (rhizomes as well as aerial stem of *E. arvense*, aerial stem only of *E. sylvaticum*), (b) two endodermes, one outside and one inside the ring of bundles (rhizome of *E. sylvaticum* and aerial stem of *E. hyemale*), and (c) a separate endodermis around each vascular bundle (aerial stem and rhizome of *E. fluviatile* and rhizome of *E. hyemale*).

The vascular bundles of *Equisetum* are unique structures and there are contrasting view points about their nature. In a very young bundle, the protoxylem is towards the inner face. In a mature bundle, these elements get disorganized and lie on the periphery of protoxylem lacuna or carinal canal (Fig. 4.2 E). In radial alignment with carinal canal is phloem; composed of phloem parenchyma and sieve tubes with sieve plates on diagonal walls. Flanking the phloem and spatially separated from protoxylem are two groups of xylem elements. These xylem groups have been described as metaxylem. More appropriately, they should be described as lateral xylem as they have protoxylem elements and occasionally their own protoxylem lacuna, as in *E. sylvaticum* (Bierhorst, 1971). In *E. arvense* are present tyloses on metaxylem (Saxena, 1992).

A vascular bundle has been described to be endarch on the assumption that protoxylem elements represent a continuation of metaxylem (lateral xylem). On the contrary, studies based on young internodes have revealed that the bundle is mesarch and the evidence gets lost by the expansion of carinal canal. The protoxylem and metaxylem elements have annular and helical thickenings or have circular bordered pits.

Some species have true vessels. They are either simple perforation plates or are reticulate. These vessels are, however, restricted to internodal regions and do not form conducting channels as in flowering plants. The carinal canal is also conducting in function. It can be demonstrated, by placing an actively growing shoot, in a dye solution. The movement of dye is primarily through the canal.

The only mature tissues of the stem, traceable to apical meristem, are carinal xylem and protophloem. All other mature cells are the products of intercalary meristem (Bierhorst, 1971). In a transection of stem passing through intercalary meristem. (Fig. 4.2 F) is seen meristematic collenchyma which gives rise to cortical sclerenchyma. In it can be seen protophloem and protoxylem lacuna.

At a node, neither are vallecular canals nor carinal canals. The central region is not hollow and instead there is a pith diaphragm. The stele is a continuous cylinder of xylem (Fig. 4.1 F) from which arise leaf traces and branch traces. At the level of leaf attachment there is trichotomy of protoxylem. The median bundle enters the leaf. The two laterals diverge right and left and meeting the adjacent lateral joins with it to form vascular bundle of internode.

The leaf mesophyll is lacunate and there is a median mesarch vascular bundle. The cells of abaxial epidermis on their outer tangential walls have various types of ornamentation patterns. Stomata form longitudinal rows. On the adaxial surface of leaf, along the mid-vein region, are hydathodes.

The roots are slender and grow by means of an apical cell, the outermost derivatives of which form the root cap. Root stele has 2-6 protoxylem points surrounding a single central metaxylem element (Fig. 4.2 G). In between protoxylem elements is the phloem. The root in the genus has been described to have double endodermis but the cells of inner row are without casparian strips and therefore should be called pericycle. Root of *E. ramossisimum* unlike other species, bears paired branched root hairs (Saxena, 1992).

Stoma in *Equisetum* is a highly specialized structure; both guard cells and accessory cells regulate its opening. In the formation of a stoma, a protoderm cell divides by two successive longitudinal walls into three cells. The two laterals are crescent-shaped accessory cells and the middle one the guard mother-cell. Following the production of guard cells, the accessory cells grow over and completely overarch the guard cells in such a way that they appear to be a result of periclinal division (Fig. 4.2 C). On the lower surface of accessory cells develop a number of siliceous thickenings and they appear to radiate from stomatal pore (Fig. 4.2 D).

Reproduction

The cones (Fig. 4.3 A) are terminal either on the main shoot as in *E. arvense* (Fig. 4.1 A, B), or on smaller lateral branches as in *E. hyemale*. At the base of cone is a ring like structure, the annulus or collar, formed by the complete fusion of sterile appendicular structures. Occasionally, and especially in *E. arvense* the axis continues to grow and forms indeterminate structure. In some species is shoot dimorphism (sterile and fertile shoots). Vegetative shoots are green and branched and fertile cone-bearing-shoots are brown and unbranched in *E. arvense* and *E. sylvaticum*. In the latter the fertile shoots turn green on shedding of spores, green branches grow from nodes of brown unbranched shoot.

The cones are made up of compactly arranged whorls of peltate appendages, the sporangiophores. At successive whorls the

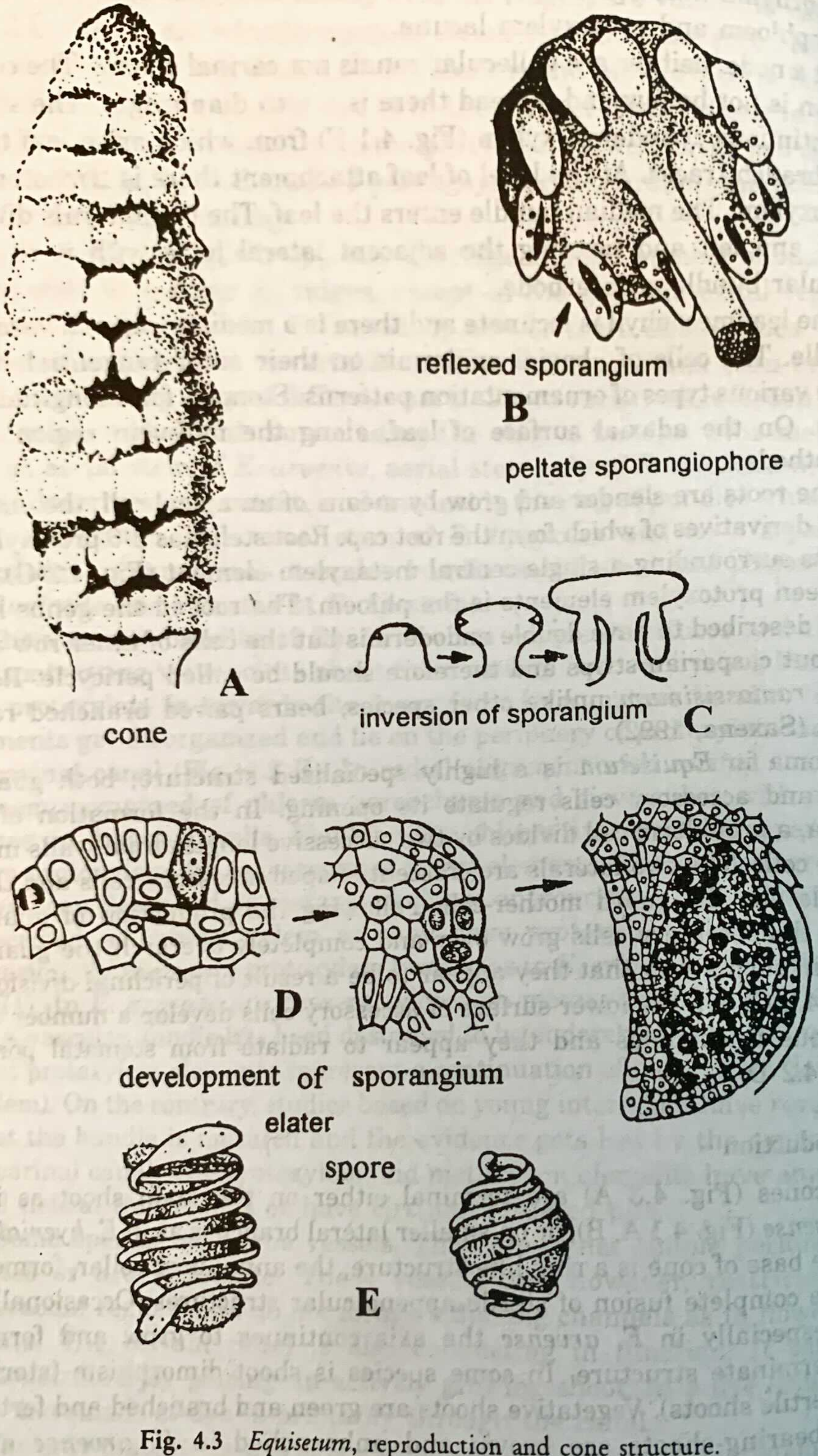

Fig. 4.3 *Equisetum*, reproduction and cone structure. A, mature cone. B, *E. telmateia*, a sporangiophore. C, diagrammatic representation of inversion of a sporangium. D, development of a sporangium. E, mature spores with elaters (uncoiled and coiled).

sporangiophores alternate but somewhat irregularly, due to condensation of axis. Each sporangiophore (Fig. 4.3 B) has a slender stalk by which it is attached to the strobilus axis and its free distal end is expanded into an hexagonal disc. The discs of sporangiophores at the basal and apical regions are of different configurations to suit the shape of cone (Fig. 4.3 A). On the underside of the sporangiophore disc (Fig. 4.3 B) are borne 5-10 elongate sporangia with their round apices facing the central axis. The sporangiophores have been variously interpreted as sporophylls, stems or other organs.

In the cone axis, there is greater development of internodal xylem with relatively less xylem at the nodes resulting in a netted appearance, and without large canals as seen in stem. The vascular supply to the sporangiophore arises from the nodal ring of the cone axis and after traversing up to the end of stalk it dichotomizes to supply one trace to each sporangium.

The primordia of sporangiophores are dome-shaped (Fig. 4.3 C) and develop at the apex in position where leaf primordia are formed, on vegetative apices. Sporangial initials differentiate on the dome of sporangiophore apex very early, and later with the expansion of the dome the sporangia are pushed to the underside of the disc.

Sporangia are eusporangiate. However, all sporogenous tissue can be traced to a single initial (Fig. 4.3 D). Therefore, it has been questioned whether the sporangia originate from one cell or a group of cells (Fagerlind, 1961).

The jacket of a developing sporangium is several cells in thickness, the inner layers of which function as tapetum. In a mature sporangium the jacket is only two cell layers. Cells of the outer layer have spirally thickened walls. As the sporocytes are formed the walls of tapetal cells breakdown and their contents fuse forming periplasmodium. Before reduction division, about one third of the sporocytes also disintegrate and their contents get mixed up with that of tapetal cells forming a plasmodial liquid. The developing spores soon become spherical and come to have very elaborate wall structure, mainly due to the activity of periplasmodium.

As the spores mature, four acellular strap-shaped bands with spoon-like tips are deposited on their outer surface (Fig. 4.3 E). These bands are attached at a common point and are hygroscopic, remian coiled to the spore when moist and uncoil as the spores dry. These bands are referred as elaters. Their function is, however, uncertain. Possibly, their expansion assists the sporangium in dehiscence or their contraction and expansion help in long distance dispersal of spores. The spores are large, green with a brief viability period ranging from one to fortyeight hours after dispersal. Germination on a moist substratum is possible within two days.

First division of a germinating spore is unequal (Fig. 4.4 A) and takes place within ten to twelve hours forming smaller rhizodial cell and larger prothallial cell. From the latter, by a series of unequal divisions, is

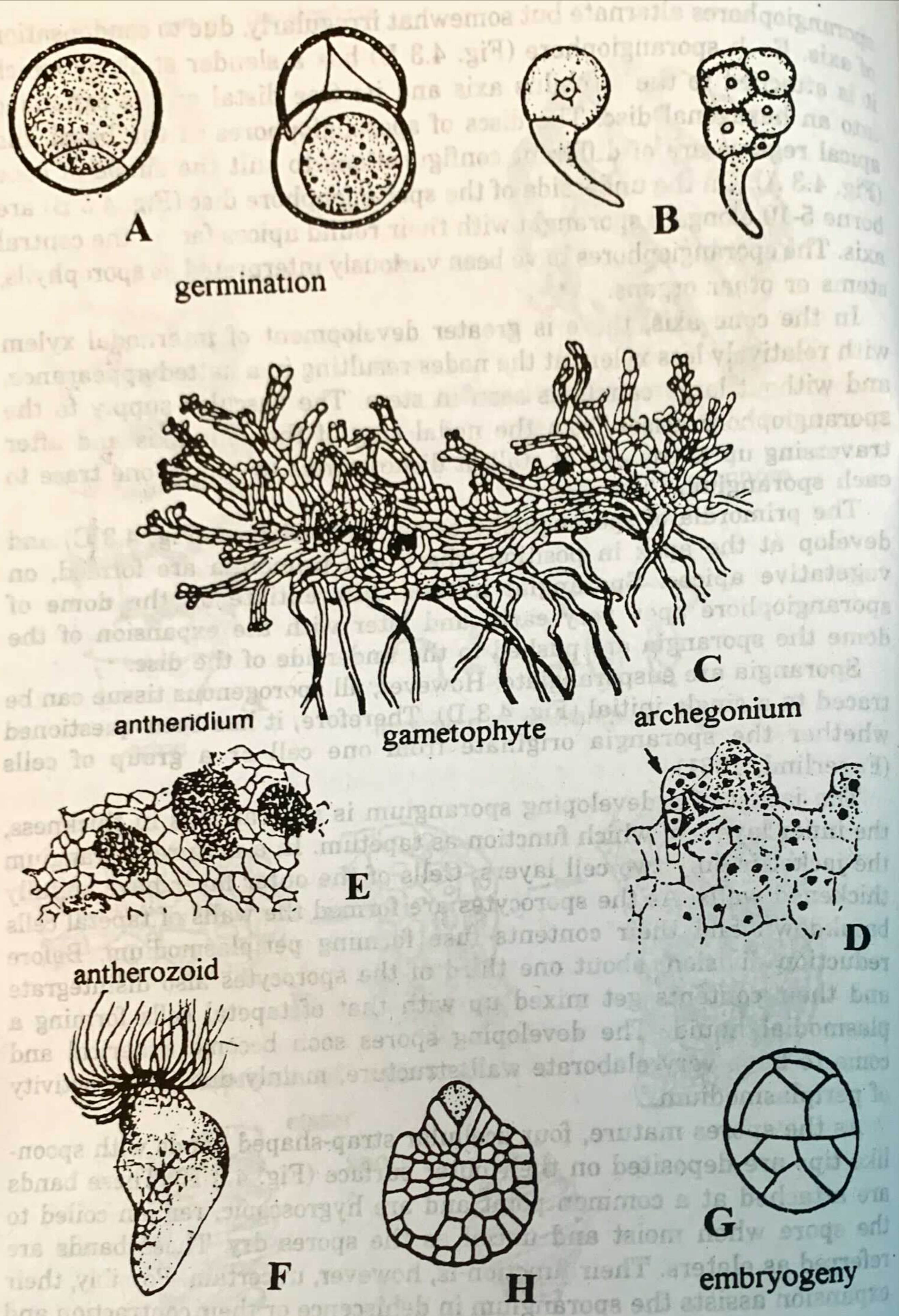

Fig. 4.4 *Equisetum*, gametophyte morphology, sex organs and embryogeny. A, germination of spores. B, initiation of gametophyte. C, *E. scirpoides*, a mature gametophyte (enlarged). D, an archegonium showing two boot-shaped neck canal cells. E, gametophyte sectioned to show elongate antherida. F, *E. arvense* a sperm. G,H, *E. arvense*, stages of embryogeny.

formed the prothallus (Fig. 4.4 B). The mature prothallus has a basal pad with upright lobes (Fig. 4.4 C). The rhizoids are borne on the undersurface of the pad. Gametophytes are green pin head cushion-like structures, often indistinguishable from moss protonema or algal growth on the river banks, but in tropical species they are compact cushion-like structures, of up to 3 cm diameter and when growing on exposed sand turn bright red.

Sex determination in *Equisetum* is influenced by environmental conditions. Incipient to complete heterothallism occurs in the genus, without accompanying heterospory. Among Latin American horse-tails, *E. giganteum* is bisexual, the gametophytes produce antheridia and archegonia simultaneously. In contrast, gametophytes of *E. myriochaetum* are either male or female. The latter, in absence of fertilization, develops antheridial lobes. The gametophytes of *E. bogotense* are unisexual and do not change sex (Hauke, 1969). Thus there is a series illustrating sexuality from bisexual condition to a unisexual condition through a transitional stage of plasticity.

The archegonia (Fig. 4.4 D) are confined to cushion region, in between the aerial lobes (Fig. 4.4 C), and project by their 3 or 4-celled high necks. The axial row consists of an egg, venter canal cell, and one neck canal cell. In some species there are two neck canal cells which are boot-shaped and lie side by side. The antheridia are embedded and elongate (Fig. 4.4 E) structures normally present on the aerial lobes but rarely also occur in the cushion region. They are massive and produce large number of spirally coiled, multiflagellate (Fig. 4.4 F) antherozoids. Each sperm has about 120 flagella (Duckett & Bell, 1977).

The embryogeny in *Equisetum* has been poorly documented (Sadebeck, 1878). The first division of zygote is transverse (Fig. 4.4 G). No suspensor is produced and the embryo is exoscopic. On the apical region is established the stem apical cell (Fig. 4.4 H). First leaves are either embryonic in origin or may form from stem apex. The root may arise from entire lower embryonic hemisphere or only from one side and the other side forms the foot.

At the end of this account of living representative of sphenopsids (*Equisetum*) and before the beginning of their fossil representatives it will be in order to draw the attention of reader towards a fossil genus *Equisetites* from carboniferous which resembles *Equisetum*.